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Multi-scale data used to analyze the spatial distribution of French grunts, *Haemulon flavolineatum*, relative to hard and soft bottom in a benthic landscape

Matthew S. Kendall[a], John D. Christensen[a] & Zandy Hillis-Starr[b]
[a]*NOAA/NOS/CCMA Biogeography Program N/SCI-1, 1305 East-West Highway, Silver Spring, MD 20910 U.S.A. (e-mail: matt.kendall@noaa.gov)*
[b]*NPS/Buck Island Reef National Monument, 2100 Church St., Kings Warf #100, Christiansted, St. Croix, U.S. Virgin Islands*

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Synopsis

We evaluated the day-time distribution of juvenile and adult French grunts, *Haemulon flavolineatum*, relative to the spatial configuration of hard and soft bottom areas in a benthic landscape. Probability of juvenile presence on hard bottom sites was inversely correlated with distance to soft bottom. Adults presence at hard bottom sites showed no significant relationship with distance to soft bottom. A significant and positive relationship was found between presence of juveniles on hard bottom sites and area of soft bottom within 100 m, but no significant relationship was found for area of soft bottom within 500 m. Adults exhibited no significant relationship with area of soft bottom for either distance tested. These distributions are suspected to be the result of the combined influence of larval settlement patterns and foraging behaviors associated with hard and soft bottom. This study indicates that data collected at very fine scales can be analyzed in the context of the broad-scale mosaic of habitats in the benthic landscape to predict patterns of fish distribution. Such spatially explicit conclusions are not possible through analysis of fine-scale or broad-scale data alone.

Introduction

In the Caribbean, research focused on habitat selection of the French grunt, *Haemulon flavolineatum*, has been conducted at fine-scales while broad-scale influences on fish distribution have been virtually ignored. These fine-scale studies in the Virgin Islands have determined that larvae settle with greater frequency on sand and seagrass substrates than onto reef and hard bottom (Shulman & Ogden 1987). After a few weeks in soft bottom residence, recruits move to nearby reefs (Helfman et al. 1982, McFarland et al. 1985). Juveniles then begin a pattern of diel migration from protective resting sites on coral reefs during the day to night-time feeding grounds consisting of seagrass beds and other soft bottom habitats such as sand and mud (Ogden & Ehrlich 1977). Juvenile *H. flavolineatum* school during the day at coral reef and other hard bottom habitats (hereafter referred to collectively as 'hard bottom') then disperse around dusk to feed solitarily throughout the night (Helfman et al. 1982). Agonistic interactions and territorial defense of preferred soft bottom feeding areas have been suggested to occur once individuals disperse at night (McFarland & Hillis 1982). Dispersal distances for juveniles are suspected to range from tens to hundreds of meters (Ogden & Ehrlich 1977), although few direct measurements of this distance have been conducted. Adults are suspected to have a similar diel migration pattern although shifted offshore and outside of protective lagoons where juveniles are concentrated (Ogden & Ehrlich 1977, Lindeman 1997).

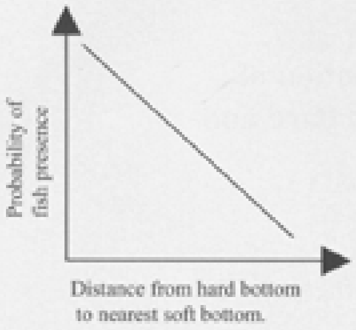

Figure 1. Expected relationship of fish presence on day-time censuses over hard bottom with distance to soft bottom.

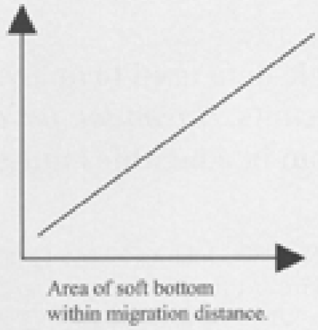

Figure 2. Expected relationship of fish presence on day-time censuses over hard bottom with area of proximal soft bottom.

Despite these studies on the fine-scale (1–10 m) habitat preferences and behaviors of juvenile grunts much uncertainty remains about their broad-scale (>100 m) home range, migratory distances, and other interactions with the benthic landscape. Furthermore, little concrete evidence exists on adult home ranges or on the spatial relationship between adult distribution and the configuration of hard and soft bottom habitats at any scale. While it is assumed that adults exhibit a similar diel pattern of habitat use to that of juveniles although shifted offshore (Ogden & Erlich 1977), this has not been thoroughly evaluated. Two interesting tagging studies provide some data on these behaviors for adults but were unfortunately limited by small sample size (Tulevech & Recksiek 1994, Burke 1995).

In addition to the findings from fine-scale observational studies, optimal foraging theory predicts that during the day both juvenile and adult *H. flavolineatum* will utilize hard bottom refuges that are in close proximity to soft bottom feeding grounds such that energy expended on traveling between resting sites and foraging sites is minimized (Pianka 1988) (Figure 1). Furthermore, larger areas of soft bottom adjacent to hard bottom resting sites should support a larger population of grunts at resting sites since larger areas of soft bottom provide more potential space for nocturnal foraging activities of solitary grunts (Figure 2).

In this study, we analyzed day-time fish census data in combination with digital maps of the benthic landscape to evaluate the spatial distribution and scales at which *H. flavolineatum* responds to hard and soft bottom in the benthic landscape. Using this process, the following hypotheses were evaluated: (1) juvenile and adult *H. flavolineatum* are more frequently observed at hard bottom sites rather than soft bottom sites during the day, (2) adult *H. flavolineatum* are more frequently observed at offshore (bank) sites rather than inshore (lagoon) sites during the day, (3) adult and juvenile *H. flavolineatum* have a higher probability of occurrence during the day on hard bottom habitat that is in close proximity to soft bottom, and 4) adult and juvenile *H. flavolineatum* have a higher probability of occurrence during the day on hard bottom habitat that is within diel migration distance of large areas of soft bottom.

Methods

We conducted 120 spatially-independent visual censuses of the fish communities around Buck Island Reef National Monument, St. Croix, U.S. Virgin Islands in February 2001 (Figure 3). In this census technique, a diver affixes one end of a 25 m tape to the substrate and then swims a random compass heading while recording all fish species, their size, and abundance observed within 2 m of both sides of the transect line until all 25 m of the tape have been uhreeled. Once the censuses were completed, all *H. flavolineatum* sightings over 5 cm were separated into juveniles or adults based on 15 cm standard length (Gaut & Munro 1983) and then scored as either 'present' or 'absent' at each census site. Newly settled larvae and early juveniles less than 5 cm are difficult to distinguish from congeners using visual census techniques and so were not included in this analysis (Lindeman 1986). Census sites were stratified by 3 habitat types (unconsolidated sediment, submerged vegetation, and coral reef/hard bottom; Kendall et al. 2001) and position relative to a fringing reef that separates a protected lagoon from seaward sites on the insular shelf (Table 1). Each census was conducted in less than 20 m depth and entirely within an area

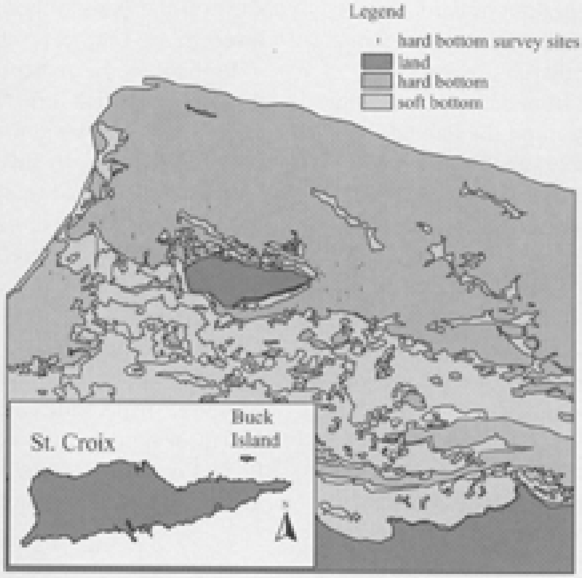

Figure 3. Bottom types within the study area, Buck Island Reef National Monument, St. Croix, United States Virgin Islands (17°47′N, 64°37′W).

Table 1. Number of independent fish censuses by location and substrate type. Bank/Shelf refers to areas seaward of the lagoon. Lower fish abundance and diversity were expected at the sand and seagrass sites within the lagoon.

	Sand	Seagrass	Coral reef/ Hardbottom
Bank/shelf	24	24	24
Lagoon	12	12	24
Total	36	36	48
Grand total			120

of homogeneous habitat type. Habitat boundaries and transition areas were eliminated during random selection of census sites. Geographic position of each census site (±1 m) was recorded.

First, we compared the presence/absence of adults and juveniles between soft bottom (sand and seagrass) and hard bottom censuses (Fisher's Exact Test, SAS Institute 2000) to evaluate the null hypothesis that there is no difference in the presence/absence ratio of *H. flavolineatum* by bottom type. This was done to confirm that *H. flavolineatum* preferentially utilize hard bottom over soft bottom sites during the day. In addition, we compared the presence/absence of adults and juveniles between lagoon and bank sites (Pearson's Chi Square Test, SAS Institute 2000) to evaluate the null hypothesis that there is no difference in presence/absence ratio between lagoon and bank/shelf sites. This was done to validate the common supposition that adults are found primarily offshore outside the lagoon. Finally, we used the 48 hard bottom census locations and associated presence/absence values to evaluate the relationship between the distribution of adult and juvenile *H. flavolineatum* and (1) distance to nearest soft bottom as well as, (2) total area of soft bottom within diel migration distance from hard bottom census sites.

We evaluated these aspects of *H. flavolineatum* distribution by examining the spatial position of each hard bottom census site relative to soft bottom areas on benthic maps of the study area. NOAA's Biogeography Program (2002) created benthic maps of the study area by visual interpretation of bottom features from aerial photographs. A total of 26 habitat types were mapped within three broad categories: unconsolidated sediment, submerged vegetation, and coral reef/hard bottom (complete descriptions are available in Kendall et al. 2001). For this analysis, we grouped these map categories into either hard bottom (coral reef/hard bottom) or soft bottom (unconsolidated sediment, submerged vegetation) since these are the two general habitat types that grunts interact with (Figure 3). We determined the relationship between fish presence and the spatial configuration of hard and soft bottom on the landscape by overlaying the location of each fish census on the habitat map.

First, we measured distance from each hard bottom census site to nearest soft bottom on the habitat map. We evaluated the relationship between this distance and juvenile and adult *H. flavolineatum* presence/absence observed at those hard bottom census sites using logistic regression. Second, we measured the total area of soft bottom (in square meters) within probable migration distance from each hard bottom census site. We evaluated the relationship between this area and juvenile and adult presence/absence using logistic regression. Since only rough estimates of migration distance are available for *H. flavolineatum* (Ogden & Erlich 1977, Burke 1995) we explored two values, 100 and 500 m, which cover the range of migration distances suggested for this species in the literature.

Results

We found a strong dependence between the presence of *H. flavolineatum* and bottom type. We observed both juveniles and adults significantly more often at hard bottom sites than soft bottom sites (Fishers Exact Test, 2-tail; juveniles $p < 0.0001$; adults $p < 0.0001$; Tables 2 and 3). However, trends in presence/absence of juveniles and adults were less dramatic when lagoon and bank sites were compared. Presence of juveniles was significantly dependent on location. Juveniles were found more frequently at lagoon sites ($\chi^2 = 4.00$, $p = 0.04$; Table 4) than bank sites. Similarly, we found adults at sites in the lagoon more frequently than at sites on the bank although at a slightly higher alpha level ($\chi^2 = 3.38$, $p = 0.06$; Table 5).

Probability of fish presence at hard bottom sites depended on fish life stage and the spatial parameter examined. A significant relationship was found between presence of juveniles and distance from hard bottom census sites to soft bottom ($\chi^2 = 5.11$, $p = 0.02$, Figure 4). Probability of juvenile presence at census sites was inversely related to their distance from soft bottom. In contrast, presence of adults was not related to distance of hard bottom census sites to soft bottom ($\chi^2 = 0.19$, $p = 0.66$).

There was also a significant relationship between presence of juveniles and area of soft bottom within 100 m of hard bottom census sites ($\chi^2 = 4.75$, $p = 0.02$; Figure 5) but not between presence of juveniles and area of soft bottom within 500 m ($\chi^2 = 0.09$,

Table 2. Contingency table analysis of juvenile presence/absence by hard bottom *versus* soft bottom. Fisher's exact test (2 tail) $p < 0.0001$.

	Present	Absent	Total
Hard bottom			
Count	16	32	48
Total %	13.33	26.67	40.00
Column %	80.00	32.00	
Row %	33.33	66.67	
Soft bottom			
Count	4	68	72
Total %	3.33	56.67	60.00
Column %	20.00	68.00	
Row %	5.56	94.44	
Total	20	100	120
	16.67	83.33	

Table 3. Contingency table analysis of adult presence/absence by hard bottom *versus* soft bottom. Fisher's exact test (2 tail), $p < 0.0001$.

	Present	Absent	Total
Hard bottom			
Count	22	26	48
Total %	18.33	21.67	40.00
Column %	88.00	27.37	
Row %	45.83	54.17	
Soft bottom			
Count	3	69	72
Total %	2.50	57.50	60.00
Column %	12.00	72.63	
Row %	4.17	95.83	
Total	25	95	120
	20.83	79.17	

Table 4. Contingency table analysis of juvenile presence/absence by lagoon *versus* bank/shelf. $\chi^2 = 4$, $p = 0.04$.

	Present	Absent	Total
Bank/shelf			
Count	8	64	72
Total %	6.67	53.33	60.00
Column %	40.00	64.00	
Row %	11.11	88.89	
Lagoon			
Count	12	36	48
Total %	10.00	30.00	40.00
Column %	60.00	36.00	
Row %	25.00	75.00	
Total	20	100	120
	16.67	83.33	

p = 0.76). Presence of adults showed no significant relationship with area of soft bottom for either distance from hard bottom sites (100 m, $\chi^2 = 0.53$, $p = 0.46$; 500 m, $\chi^2 = 0.05$, $p = 0.82$).

Discussion

As expected, both juvenile and adult *H. flavolineatum* were found primarily over hard bottom substrates during the day. This habitat preference has been well documented by a number of studies and is presumed to offer grunts structural refuge from day-time predators. Only when light conditions at dusk and higher visual acuity of grunts in dim light favor avoiding predators do juvenile grunts venture to open soft bottom to feed (McFarland et al. 1979). Also as expected, juveniles were found primarily in lagoon areas which are suspected to act as nurseries to early life stages of many reef species. However, adults were no more likely to be found offshore than in the lagoon as had been previously speculated (Ogden & Erlich 1977) and in fact were more likely to be found at lagoon sites at the alpha 0.06 significance level. Additional census data and higher power of statistical tests are needed to further resolve the inshore–offshore distribution of adults in this study area. Researchers in nearby Puerto Rico have documented the inshore to offshore shift in adults suspected by Ogden and Erlich (1977) although they found adults to be more evenly spread across the shelf than juveniles (Dennis 1992, Lindeman 1997). It is also possible, however, that the abundance of adults outside the lagoon in our study area is artificially low due to increased fishing pressure on the bank. A recent study documented higher fishing effort outside the Buck Island National Monument boundaries on the bank than inside the boundary which includes the lagoon. Furthermore, the study found a decrease in size and abundance for most predatory fishes in this area as a result of the trap fishery (Beets 1996).

Previous research on grunt distribution indicated that fish abundance was higher on reefs in close proximity to seagrass beds (Randall 1963, Ogden & Zieman 1977), however, rigorous analysis of the spatial scale of this association was not possible due to the lack of adequate benthic landscape maps. By analysis of fine-scale fish/habitat associations in the context of broad-scale maps of the benthic landscape, this study indicates that

Table 5. Contingency table analysis of adult presence/absence by lagoon *versus* bank/shelf. $\chi^2 = 3.3$, $p = 0.06$.

	Present	Absent	Total
Bank/shelf			
Count	11	61	72
Total %	9.17	50.83	60.00
Column %	44.00	64.21	
Row %	15.28	84.72	
Lagoon			
Count	14	34	48
Total %	11.67	28.33	40.00
Column %	56.00	35.79	
Row %	29.17	70.83	
Total	25	95	120
	20.83	79.17	

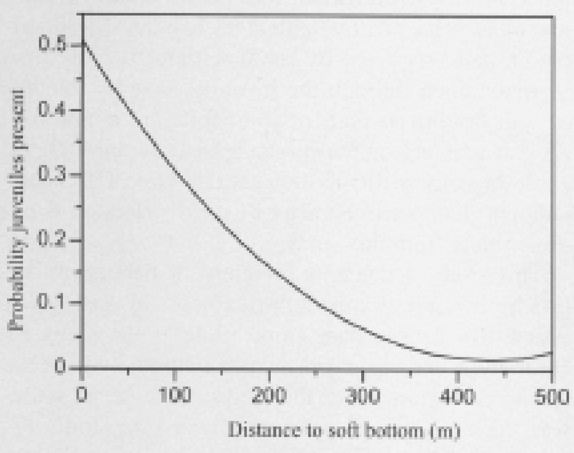

Figure 4. Logistic regression of juvenile presence by distance (m) from hard bottom census site to soft bottom. $\chi^2 = 5.11$, $p = 0.024$.

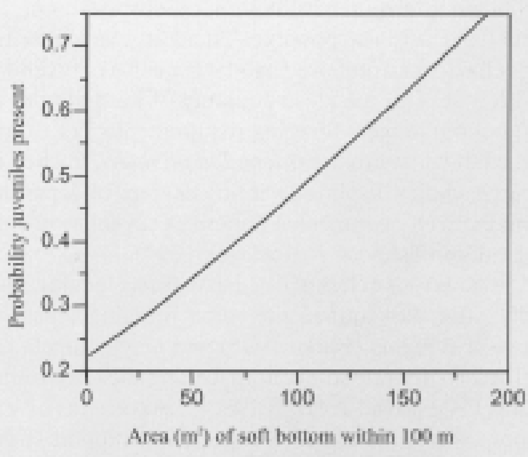

Figure 5. Logistic regression of juvenile presence/absence by area of soft bottom within 100 m. $\chi^2 = 4.75$, $p = 0.029$.

probability of juveniles being present at hard bottom sites is higher the closer those sites are to soft bottom. Juveniles may be distributed in this way to limit the distance that they must travel to nocturnal feeding sites. This would minimize unnecessary energy expenditures on diel migration and maximize time allotted to foraging. A plot of the line generated from the logistic regression model of these data indicates that an asymptote in predicted probability of presence of juveniles is reached at a distance of 300 m from soft bottom. Probability of juvenile grunts being found on hard bottom sites greater than 300 m away from soft bottom is near zero. Hard bottom sites in excess of this distance to soft bottom may be structurally similar to hard bottom directly adjacent to soft bottom, yet unsuitable as daytime habitat for juvenile grunts since traveling hundreds of meters to and from suitable foraging habitat each day would needlessly expend energy.

Presence of adults on the other hand, was not observed to have a significant relationship with distance of hard bottom resting sites from soft bottom. This may be the result of a lack of a sufficiently large range of distances in the sampling data. The larger adult fish may simply have a larger migration range than juveniles (Kramer & Chapman 1999). If the migration range for adults were larger than the maximum distance between hard bottom and soft bottom sites of this study it would explain the lack of both significance and an asymptote from being reached in the analysis of the adult data as was found for juveniles. Only by including census sites with a hard bottom to soft bottom distance that is in excess of the migration distance for adults might a significant decrease in probability of finding adults on hard bottom be observed. On the other hand, it is also possible that adults change foraging behavior and preferred habitat from that of juveniles and rely less on the close coupling of hard bottom to soft bottom to meet foraging requirements. For example, adult white grunts, *Haemulon plumieri*, tracked in tagging studies displayed varying degrees of departure from the well documented pattern of juvenile off-reef migrations (Tulevich & Recksiek 1994).

Previous research suggested that grunts feeding solitarily after dark utilize the same foraging areas on successive nights (Burke 1995) and may compete for and defend discrete soft bottom feeding sites from other grunts (McFarland & Hillis 1982). Larger areas of soft bottom would therefore be expected to support larger numbers of grunts. The distances over which grunts respond to area of soft bottom are poorly understood and can be inferred only from tagging studies with few replicates (Tulevech & Rechsiek 1994, Burke 1995). Since home range size is often a function of fish size (Kramer & Chapman 1999) analysis of the area of soft bottom within migration distance from hard bottom census sites was conducted at two scales (100 and 500 m) in an attempt to evaluate the spatial determinants of suitable grunt habitat for smaller (juvenile) and larger (adult) fish. It was found that presence of juvenile *H. flavolineatum* was positively correlated with amount of soft bottom foraging area within 100 m of day-time resting sites but not with soft bottom within 500 m suggesting that maximum migration distance for juveniles lies between these two values. This is in agreement with the observation that juveniles were not likely to be found on hard bottom sites in excess of 300 m from soft bottom. However, presence of adults was not significantly correlated with area of nearby soft bottom at either spatial scale tested. Again, this may suggest a de-coupling of adult reliance on soft bottom/hard bottom foraging migrations or the results may be limited by the spatial range in this data.

Additionally, *H. flavolineatum* distribution on hard bottom could initially be influenced by patterns of larval settlement. Observations in St. Croix indicate that larvae settle with greater frequency on sand and seagrass substrates than directly onto the reef (Shulman & Ogden 1987). Only after a few weeks of soft bottom residence do recruits move to nearby reefs and begin diel foraging migrations (Helfman et al. 1982, McFarland et al. 1985). Hard bottom sites in close proximity to large areas of soft bottom could have higher occurrence of *H. flavolineatum* due to the influx of early juveniles from nearby settlement habitat. The distribution pattern caused by larval settlement could then be maintained through the juvenile stage by reliance on soft bottom habitat for short foraging migrations. As fish size and migration range increase through the adult stage, these distribution patterns appear to change although the exact character of the distribution is not discernable from this study.

This study documents a pattern of habitat utilization by juvenile grunts not discernable by analysis of visual fish census data alone (Sale 1998). Only by combining fine-scale census data with analysis of the spatial configuration of the landscape at broad-scales was the association apparent between day-time distribution of juvenile grunts and hard bottom in close proximity to large areas of soft bottom. While the logistic regression models used here revealed some significant relationships, a large amount of variability in the determinants of grunt distribution remains unexplained. Several modifications to this approach should be explored to improve model results. For example, more detailed habitat types could be included in the analyses from among the original 26 categories in the benthic maps. Since all hard bottom and soft bottom sub-categories in the original benthic maps are not likely to be of equal value to grunts as day-time resting sites and night-time foraging areas respectively, including more detailed habitat categories in the analysis should further elucidate grunt distribution in the landscape. Other environmental variables such as depth and distance from shore should be included in future analyses as well since those factors are also known to influence grunt distribution (Lindeman 1997). In addition, the spatial spread of sample sites on future fish censuses should be increased to include census sites farther from soft bottom habitats. Including sites farther from soft bottom would allow evaluation of relationships between adult grunt distribution and landscape elements that occur at broader-scales. Finally, this study focused only on day-time distribution of grunts, their night-time foraging activities could be modeled similarly once adequate information is obtained on these migrations at fine-scales.

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